

XXIII. *On Heterogynis paradoxa, Embr., an instance of variation by segregation.* By THOMAS ALGERNON CHAPMAN, M.D.

[Read October 1st, 1902.]

PLATE XXVIII.

SOME years ago I had an opportunity of studying *Heterogynis penella*, and reported some of my observations to this Society (Trans. 1898). I had then no knowledge whatever of *H. paradoxa*, nor any particular hope of ever acquiring any. It was therefore with some pleasure that I came across the species this summer in sufficient numbers to enable me to become familiar with it in several aspects, and some of these seem to be of sufficient interest to be worth reporting.

The two species of *Heterogynis* are very much alike, so much so, that to question whether they are really distinct is by no means an irrational attitude. In all those points which makes the genus so interesting they seem to be identical, such as the curious specialization of the female pupa-case; the organic attachment to, and continuity of, the female moth with the pupa-case at the points where the true legs should exist, this attachment being the only trace of appendages the female moth has; her exact agreement in colouring with that she possessed in the larval state, differing in appearance from the larva only in being smooth and glistening, instead of dull and possessed of tubercles and fine hairs. They are the same also in the way in which the female moth emerges from her cocoon, and rests on the opened top of the pupa-case which partially protrudes from the cocoon, in pairing lasting only for some thirty seconds, and the moth retreating thereafter in five or six minutes into her pupa-case, and in this falling back into the cocoon. If the moth has been out of her pupa for some time, she takes a somewhat longer time to make her retreat. In both species the young larvæ when hatched eat up the remains of the parent moth, and then are possessed by an intense desire to wander. They then feed for a time, and hibernate by spinning a small

cocoon in some crevice of the food-plant or elsewhere. *H. paradoxa* does this, I find, in the second instar; Mr. Fletcher found *H. penella* did so in the third. Whether there is here a real specific distinction I cannot say, or whether there may be an error of observation on my part or on Mr. Fletcher's. The newly-hatched larva of *penella* is certainly much smaller than that of *paradoxa*.

On all these points and some others my observation of *H. paradoxa* yielded nothing that I had not already noticed in the case of *H. penella*, and of these I do not propose to go into any further details.

The circumstance round which most of my interest in *H. paradoxa* gathered, was in there being no less than three forms or races of the species met with in the small district in Spain we examined.

Bejar, which Mr. Champion and I made our headquarters this summer for three weeks, is in a granite region, and is some 3300 feet above the sea. Above it the Sierra de Bejar rises to a height of nearly 8000 feet, and snow lay there in quantity up to the end of July, and does so in places I believe throughout the year. Brooms of half-a-dozen species are a very special feature of the vegetation here. *Genista florida* very much beautified the undergrowth in the neighbourhood of Bejar, but not going higher than 4000 feet at the outside. On the Sierra, *Cytisus purgans* begins about 5000 feet and goes up to nearly the top of the Sierra; it does not thrive or flower freely at its lower levels, but at about 6000 feet we found it forming dense masses of bloom covering thousands of acres, and most plants were not simply sheets of bloom but solid masses. Mr. Champion found, I think, that with the beetles, it was an exceedingly marked feature of the fauna that everything lived on the broom; this fact was not perhaps quite so striking in the *Lepidoptera*, but it was very marked. At any rate these brooms it was that made *Heterogyris paradoxa* one of the notable *Lepidoptera* of the region.

The first evening of our arrival at Bejar, viz. June 26th, I met with *H. paradoxa*, it was then fully out, and occurred close to Bejar at an elevation of about 3500 feet. The males were most easily found by looking over the plants of *Genista florida*, on the more elevated and separate twigs of which they were at rest, with their wings in some degree curled round the twig. If disturbed slightly, they

flew to a neighbouring twig, crawled up it, and settled down in the same way, but if really frightened, they would soar for a minute or two, and if there was any wind were liable to be carried right away. Only one or two were seen, early in the day, that were flying, without having apparently been disturbed. I took some more the following day, but a few days after had difficulty in finding one or two; it was in fact practically over, although a larva or two (ichneumonid?) could still be seen. Its period of flight is therefore (in a late season) from about June 20th—30th. To avoid circumlocution I propose to call this form of *H. paradoxa*—var. *Bejarensis*.

On July 3rd, on the Sierra de Bejar, above Candelario, at a height of perhaps 5000 feet, I took several larvæ of a *Heterogynis* on *Cytisus purgans*, which grew from about that elevation up to fully 6500 or thereabouts—a species that clothed large areas of the Sierra, and made a mass of most splendid bloom at about 6000 feet, but below was already out of flower and had apparently bloomed there but sparsely. I took two or three more larvæ later. On July 12th these larvæ produced two ♀ imagines. So on the 16th I visited the locality to see if I could not capture some males. Sembling was of no avail, but I succeeded in capturing two or three dozen specimens. Only one or two of these were taken by observing them at rest, nearly all being disturbed by walking through and beating the broom bushes. The proportion of worn specimens showed they were a day or two past their best. This variety I call *Candelaria*.

Later still, July 18th, at Piedrahita, some twenty-five or thirty miles from Bejar, and on an outlying ridge of the Sierra de Gredos, separated from the Bejar range by a rather wide valley, I met with a third form of *Heterogynis*. It was then only just coming out at its lowest levels, at its highest, 600 to 1000 feet higher up, only larvæ were to be seen. This form (*Piedrahita*) is therefore at least ten days later than *Candelaria* in the date of its appearance. The chief interest attached to these three groups or colonies of *H. paradoxa* occurring within a limited region at successive dates, lies in the circumstance that each colony presented very definite characters by which it was distinguishable from the others.

Each group is thus probably entitled to a separate name on its merits; for convenience in speaking of them, how-

ever, it is almost a necessity, and so I have called them respectively var. *Bejarensis*, from Bejar on *Genista florida*, var. *Candelaria*, from the Sierra above Candelario on *Cytisus purgans*, and var. *Piedrahita*, from the Sierra above Piedrahita, also on *Cytisus purgans*.

In average size *bejarensis* resembles the other two forms, viz. about 25 m.m., but ranges from 20 m.m. to 29 m.m., having a larger proportion of large and small specimens, is in fact more variable in this respect. The colour is a pale, diaphanous Indian-ink tint.

The larva is very similar to a medium-tinted one of *H. penella* in colouring, but like the other two forms, and unlike *penella*, it is fairly constant in colouring, no specimens ranging far from the average, whilst *penella* had no definite type, and specimens varied much in the proportions of yellow and black markings, some even being almost entirely black, others nearly without black markings. *Bejarensis* has a dorsal black line, or rather stripe, the subdorsal yellow band has two dark spots on each segment. The next dark band is well pronounced, and is connected by dark markings with the narrow dark line below, that runs along the spiracles; below this is an uninterrupted yellow band, and below this a dark band well defined above, below irregular, and more or less reaching to the prolegs.

The cocoon is dark-coloured, the male pinkish-orange (*penella*, lemon-yellow), the female deep orange almost red. The female cocoon is of very large size compared with that of *penella*. The female cocoon is placed conspicuously on the food-plant, sometimes on a separate projecting twig such as the male imago selects as a resting-place. The male cocoon, on the other hand, is usually well hidden, so much so that I only succeeded in finding one containing a living pupa, and only perhaps half-a-dozen altogether hidden away under stones, etc., all, perhaps, but the one living one, being remains from previous years.

The food plant was a broom *Genista florida* rather abundant close to Bejar, where it made a handsome show, but of which we saw little elsewhere. Amongst it grew another broom which was very close to, if not identical with common English broom. It occurred on this also, but very sparingly as though able to live on it when the larva had wandered on to it and had no choice, but neither liking nor thriving on it. It did not occur on other

brooms also growing close by, nor on any other plant, differing therein from *penella*, which prefers common English broom, has no objection to almost any leguminous plant, and is even almost omnivorous.

The form *candelariæ* appearing a full fortnight later than *bejarensis*, was a trifle smaller than that variety, and had not so great a range in size, varying from 22—26 m.m. in expanse, and averaging 24 m.m. The colour was distinctly lighter, a smoky-brown rather than a translucent black. Their habit of resting so as to be unseen, contrasted strongly with that of *bejarensis* and of *pedrahitæ*; the food-plant is the same as that of *pedrahitæ*, and though it does not afford such spray-like branches to rest on as the *G. florida* does, *pedrahitæ* always rested in the same manner as *bejarensis*. It is to be noticed that *candelariæ* thus hides itself as an imago, as well as a pupa; and so far as my observation went, as a larva also, as I found very few of these, but this might be due to my being too late for them. As compared with *pedrahitæ* on the same food-plant, it is to be observed that *candelariæ*, as an imago to be stirred up out of its food-plant, but not to be seen at rest, was, on a certain small area of a few hundred acres, very much more abundant than either of the other varieties in a similar space, but outside this small area it was not seen at all, although its food-plant extended a thousand or two feet higher up in the greatest profusion, as well as over other ground at the same level; whilst *pedrahitæ* occurred wherever the food-plant grew, over a large area extending both vertically and horizontally.

One is inclined to suggest that the bright lemon-yellow of the larva of var. *candelariæ* is correlated with the denser yellow masses of the flower of its food-plant, and that we saw nothing of it higher up where the broom was in flower, because it was so well hidden. This may very well be so, and it may have little bearing on the point that *pedrahitæ* on the same food-plant was not at all so hidden in any stage, nor was the larva modified in colouring like that of *candelariæ*.

The larva is quite yellow, the black-green markings being much reduced, only about a dozen larvæ were taken, but were all constant in this coloration. The ♀ moths bred from them agreed with them exactly in coloration as is the case in all specimens of the genus. This pale

larva is similar to the very palest that occur in *H. penella*, in which the larva varies much in coloration. It contrasts strongly with the much darker and unvarying larva of *bejarensis*, and with the palest forms of the dark, but less constant larva of *piedrahita*. The dorsal line is extremely slender, the subdorsal yellow is very wide, the subdorsal and spiracular black lines are slight and hardly connected together at all. The yellow is bright lemon colour, with no greenish suffusion from intrusions of dark spots from the black. The male moth is, as I have already referred to, more retiring in its resting habits than *bejarensis*. The pupa is, however, much more retiring. The number of males taken showed that the species must be at least quite as abundant as *bejarensis* is, yet only three or four (all injured) female cocoons were seen, and only one male one.

Piedrahita is larger than the other forms, chiefly by being of a more uniform size, and with few small and no very small specimens, ranging from 24—26 m.m., and averaging over 25 m.m. in expanse. It has not the pale colouring they have, but it is a comparatively dense black. The food-plant is apparently the same as that of *candelaria*. The larva is close to that of *bejarensis* in colouring, it varies more than they do, some specimens being almost identical with those of *bejarensis*, but none at all so pale as *candelaria*. The male imago has precisely the same habits as that of *bejarensis*, but in the matter of pupation it is closer to *penella* than to either of the other forms, ♀ cocoons being abundant and male cocoons tolerably numerous, but less so than females (the reverse of *penella*). I had about eight ♂ moths from collected cocoons, but the great mass of those I collected produced ichneumons. The healthy male larva therefore hides his cocoon more frequently than not, but does not invariably do so.

At *Piedrahita* I frequently met with larvæ spinning their cocoons, and found they did so in a very interesting manner, in those cases in which the cocoon was spun not between twigs but on the side of one. Having covered the twig sufficiently with silk, the larva, by successive series of fine loops of silk, constructs a lace-like veil on either side of the twig, and when these have attained sufficient dimensions draws them together over its back. The process is precisely the same as that adopted by *Nola* in spinning its cocoon, though *Nola* uses films of bark

fastened together edgewise of which to make the two veils, whilst *Heterogynis* uses only loops of silk.

Difference between the vars. of *H. paradoxa*, Rmbr.

<i>Pcnella.</i>		<i>Bejarensis.</i>	<i>Candelurix.</i>	<i>Piedrahita.</i>
	Time of appearance	June 20-30	July 12-20	July 18-28 and later
20-21m.m.	Size of ♂	(40 specimens) 20-29 m.m. very variable, average 25 m.m.	(45 specimens) 22-26 m.m. not much variation, average 24 m.m.	(76 specimens) 24-26 m.m. very uniform, full 25 m.m.
Very dark	Colour of ♂	rather dark	pale	very dark
Very variable	Larva, colour	rather dark, <i>i.e.</i> green-black marking strong, very uniform	very pale, <i>i.e.</i> green-black marking nearly evanescent, very uniform	pale and dark, none as pale as <i>Candelaria</i> , variable
Often hidden	Cocoon ♀	conspicuous (abundant)	hidden (found two destroyed ones)	conspicuous (abundant)
conspicuous	Cocoon ♂	hidden (found <i>one</i>)	hidden (found)	conspicuous but usually (95 p.c.) parasitised a majority of healthy ones probably hidden (bred 8 moths)

These three races of *H. paradoxa* appear to be as definitely distinct from each other, both as larva, pupa and imago, either in colour or habit or both, as if they were distinct species. Still I find it quite impossible to regard them as more than local races. Where I find something to learn from them is in considering how such definite races preserve their distinctness, although they are one species and live within a few miles of each other. In the cases of the vars. *corydonius* and *hispana* of *Lycæna corydon*, I was able to understand how one of these, *hispana*, was suitable to a limestone country, and *corydonius* to other conditions, but what I could not and do not at present understand, is how they keep distinct living on adjacent and practically sometimes on the same ground.

In the case of *H. paradoxa*, I can get a little nearer

comprehending how the three forms preserve their distinctness. It is, in fact, simply a case of segregation. Both species of *Heterogynis* are limited in their powers of dispersal by the female laying her eggs in her cocoon. All travelling from one area to another must be done by the larva. They are here in quite the same conditions as other species with apterous females. In most species with apterous females dispersal by larval migration is facilitated by a certain amount of polyphagous disposition on the part of the larva, this is certainly the case in *Orgyia* and in many Psychids. Even so, however, dispersal must be a slow process, and so far as such dispersal is concerned, it is quite conceivable that there might easily be enough separation of portions of the species even in continuous areas, to permit of distinct races arising. A further check to this, however, results from the male moth being usually very active and capable of flying considerable distances. Crossing thus readily takes place between colonies at considerable distances and imposes a serious impediment to any distinctive variation between them. In most years, a majority of adjacent colonies would thus be crossed with each other, and the result at the end of a few years would be that all colonies within a large area would be crossed with each other mediately if not immediately.

Considering the rather wide area of the range of *H. penella*, it probably, like so many other insects, has local races and varieties. But in the smaller regions within which I knew it, ranging from an elevation of 2000 feet at Digne to 8000 at Lauteret, and from Grenoble nearly to the Mediterranean, I am aware of the existence of no local variation at all comparable to that of *H. paradoxa* which I am describing. The almost polyphagous larva renders it capable of traversing, slowly of course, practically the whole of this area, and the male is I think more adventurous than that of *H. paradoxa*.

H. paradoxa is very differently conditioned; the larva is confined to a few food-plants. It is not like *penella*, polyphagous under some circumstances, nor even like it pleased with almost any leguminous plant. It must have broom, and not any broom. Out of six or seven plants that I called broom, *Cytisus* or *Genista*, and several other plants of the same and allied genera, it would eat only three, and one of these only as a substitute. There are possibly other brooms growing elsewhere in Spain that

please it, and it may even be variable in this point as in others, but it is unquestionable that at all its habitats where I met with it, each habitat was definitely and (to the larva of *H. paradoxa*) impassably circumscribed, by the limits of growth of its food-plants.

Crossing by migration of the male probably occurs, but it must be rarely. The male flies weakly, and never voluntarily undertakes a migratory excursion, but such must sometimes result from being caught by the wind.

The two races *Bejarensis* and *Candelariæ* live very close together, not more than three miles as the crow flies, but *bejarensis* is some 1500 feet lower than *candelariæ*, and on a S.E. instead of a north exposure; the consequence is that its flight is over before *candelariæ* comes out, so that the chances of any accidental crossing are much diminished if not entirely destroyed.

Piedrahita is separated by a wide valley from the two Bejar colonies, and curiously enough is even later in appearing than *candelariæ*, for no reason that I could observe, since it is at a level as low, possibly lower. At any rate any crossing with the Bejar forms must be all but impossible.

The segregation of these three forms from each other is, at any rate, if not complete, so nearly so as to make the differences between them easily accounted for by variation not swamped by crossing. There can be little doubt that the differences represent something that is or has been beneficial to each race, but here a longer study of the conditions affecting each colony would be necessary, even to plausible guessing. Why should *Candelariæ* hide itself so much more carefully than the others, as it does at all stages; as a result it appears to thrive at the one spot where I found it, but also as evidence that it has powerful enemies, it seems very restricted in habitat, whilst the other two forms are co-extensive with their food-plants. If there is anything in the suggestion that the larval colour is protective amongst the flowers of its food-plant, it is another item showing the need of protection in this form, since the flowers of the food-plant are nearly identical in colour in all cases, but with *Candelariæ* the flowers of *C. purgans* are denser than in *G. florida* and unmixed with leaves, but then *per contra* I only found the insect where the plant did not bloom freely.

The only other case in Lepidoptera where I have found

definite races due apparently to segregation from the females being apterous, is in the case of *Luffia ferchaultella*. As this species has no males, the segregation is of course even more stringent, and we find here that different races differ to the extent of having different numbers of joints in their tarsi (Tutts. Brit. Lep. Vol. II., Ent. Rec. Vol. XIII.).

Seeing that these three forms of *H. paradoxo* occur within a few miles of each other, and that the species occur over a very large area, how large I don't know, as I do not know precisely its range, but certainly I imagine several hundred miles across, there must be room for many other distinct races of the species, and the question may easily be asked whether such variations may not bridge over the difference between *H. paradoxo* and *H. penella*. Very possibly they may. It is not much use speculating, what is wanted is more knowledge of the colonies that probably exist in the northern half of Spain. Rambur named a third species, from the neighbourhood of Barcelona, but from very inadequate material. Kirby accepts this as a good species, all other authorities have treated it as merely *paradoxo*.

In the meantime the differences between *penella* and *paradoxo* are as definite as any usually considered sufficient to discriminate species. I have no hesitation in regarding them, as I know them, as abundantly distinct, even after making every allowance for the tendency of many species in Spain to be larger and paler than their northern representatives.

It may be useful to give a few notes on the differences between the species.

The newly-hatched larvæ present very important differences that have perhaps more specific value than any others.

The plate on the first thoracic segment has a dark mark of much the same form in both, but in *penella* it is darker shading on the plate, without very definite form, but shading off into the colourless part of the plate, while in *paradoxo* it is so definitely outlined that one takes it to be the actual plate of this peculiar form.

Penella has the usual tubercles with finely spiculated hairs, and the general surface of the skin is finely spiculated. *Paradoxo* has in addition a number of peculiar tubercles of which no trace exists in *penella*, these carry

no hairs, and are something very different from the true tubercles, yet when only slightly magnified they look just like them and are somewhat mystifying. The ordinary tubercle has a rather dark ring surrounding the base of the hair, and these special tubercles have also a dark ring of just the same size, and perhaps a little darker tint. This dark ring crowns a short conical column, and has about 10 to 12 sharp points round its margin. Without being at all like, they suggest the special tubercles of Limacodids. They are disposed one on either side of each of the dorsal tubercles, so that tubercles I and III with their eight attendant tubercles form a transverse row of 12 nearly equidistant points, whilst in the case of II the attendant tubercles are a little posterior to tubercles II, and so do not quite fall into a row with them.

There is a further very marked distinction between the two species, *penella* having only 7 crochets to the prolegs, whilst *paradoxa* has 11.

Paradoxa is larger than *penella*, and hibernates in second instar, *penella* in third.

In the full-grown larvæ, not having them side by side for comparison I may easily be at fault, but think there is no other difference than that of size.

The cocoons differ much in size and also in colour, that of *penella* being a pale lemon-yellow, of *paradoxa* a deep reddish-orange.

The male imagines are well defined by Rambur, Bruand, and others, in their descriptions of the species. *Penella* is smaller, darker, and much more densely scaled than *paradoxa*. This is especially noticeable in the body scaling. *Paradoxa* looks very thin and slight, and gives very much the same impression of being without scales on the thorax, whether they be absent or whether the somewhat evanescent and sparse clothing is still present, the abdomen is but little better furnished, whereas *penella* looks a solid, robust little fellow entirely in consequence of his thick fleece.

Penella has a more robust-looking antenna, with longer pectinations. The length of the pectinations persists till towards the end of the antenna, whilst in *paradoxa*, the shortening begins comparatively near the base. On both 36 pairs of pectinations may be counted; these are almost quite constant in *paradoxa*, but often vary to 32 in *penella*.

The anterior tibial spurs in *penella* arise near the middle

of the tibia, in *paradoxa* about $\frac{2}{3}$ from the proximal end, the longer spur (*penella*) being, as it so frequently is, correlated with the most plumose antenna.

I have not seen it noted that each antennal joint carries two pairs of the pectinations, so that there is only half the number of antennal joints that there at first seems to be, 2 basal and 18 (not 36) with plumules = 20 varying in *penella* to 19 and 18.

The parasites of *H. paradoxa* are very destructive to it. My notes might refer to two sets of parasites, one of *bejarensis*, the other of *piedrahita*. I believe they would be more correctly interpreted as referring to ♂s and ♀s, but the latter view would have to be modified by a strong suspicion I have, that what appear to be male cocoons are really merely the cocoons of larvæ that are to grow no larger, because they are parasitised, and so spin a small cocoon that one takes for that of a male larva, whereas it may be really a female whose growth is checked by the parasite.

However this may be, I collected many ♀ cocoons of *H. bejarensis*, and from them bred many Tachinid diptera of a smallish species (*Blepharidea* (*Ceratoharta*) *previa*, B. B.); one specimen of a larger species was also bred from a *Piedrahita* ♀ (the same species also emerged from *Orgyia aurolimbata*), also many Chalcids. No male *bejarensis* having been collected, no parasites were bred from them.

Many male, or apparently male cocoons were collected at *Piedrahita*, of which some 95 per cent. produced ichneumons. These were of two species. One spins an oval cocoon within that of the *Heterogynis*, after emerging from the larva of its host, and produces *Casinaria orbitalis*, Gra. In the case of the other, the *Heterogynis* either changes to pupa or appears to die as a larva, in both cases *Pimpla scanica*, Vill., emerges, by cutting out a lid in the dead skin of its host. In two instances at least a *Pimpla scanica* emerged from a cocoon of the *Casinaria*. As hyperparasitism is not recorded for *Pimpla* (I believe), and as the present species is a simple direct parasite on the *Heterogynis*, the hyperparasitism must here be an accident; the larva of *P. scanica*, finding its host occupied also by a larva of *Casinaria orbitalis*, solved the awkward situation by entering the body of its fellow-guest, as it must have been within the *Casinaria* when that spun its cocoon. Such at least is a possible explanation, though it involves

a rather improbable attribution of instinct to the *Pimpla* larva. Another explanation offers itself. The *Heterogynis* larva must be not unfrequently stung by both parasites as they are so common; what will happen in this case? Since no larva produced two parasites (we may assume that each species only stings a larva once, recognizing and avoiding one already stung by its own species), either they grow *pari passu*, and both perish for want of pabulum, or one destroys the other; if it does this by treating the other as part of its host's tissues and devouring it, we have again no outward indication that two parasites were at any time present. But suppose the *Casinaria* larva already well grown at the time the *Pimpla* stings its victim, then using its piercing ovipositor, it, quite by accident, as it were, pierces also and lays her egg in the *Casinaria* larva, the result would be what I observed, the *Casinaria* would be so far ahead of the *Pimpla* as to make its cocoon. The condition would be one of ordinary hyperparasitism so far as procedure goes, but as regards intention and instinct would be purely accidental. It presents, however, no matter how we explain it, a very interesting accident as affording material which might be elaborated by natural selection into true hyperparasitism.

EXPLANATION OF PLATE XXVIII.

Larva of *Heterogynis paradoxa*, Kamb. (First stage.)

Fig. 1. Dorsal view $\times 20$, showing tubercles and pseudo-tubercles.

Fig. 2. Portion of same $\times 250$. Below 1 is a tubercle; below 2 and 3, its two attendant pseudo-tubercles.